OBSERVATIONS ON THE LIFE-HISTORY AND DEVELOPMENT OF THE HYDROID, MYRIONEMA AMBOINENSE

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WITH SIX TEXT-FIGURES AND THREE PLATES

Myrionema amboinense (Pictet,* 1893) is found abundantly on Low Island, Queensland, in the shallow water along the margin of the mangrove swamp, especially the north-west corner (Key Chart of Low Isles, P. 1). The green plants *Thalassia hemprichii* and *Halimeda opuntia* are plentiful over the same area, and the hydroid grows in tufts on these plants and on the submerged roots of the mangrove trees, as well as on small sponges or on empty shells. The tufts average 1·5 cm. in height, but may be considerably taller (up to 4 cm. or more). Apart from the larger animals, such as the long snake-like holothurian, *Synapta maculata*, numbers of which creep continually along the ground, there is a smaller fauna living among the stems of *Myrionema* itself. Most characteristic is a small Tanaid crustacean *Leptochelia savignyi* (Krøyer), which is invariably present, inhabiting a gelatinous tube fixed to a part of the stalk, or sometimes crawling freely over the branches. Many small foraminifera are quite common, as well as the large conspicuous *Orbitolites complanata,* which sticks to the fronds of the two plants.

In 1913, Light* described this same hydroid under the name of *Eudendrium griffini* as occurring in shallow tide channels on the coral reef of Bantayan Island, Philippine Islands. All his descriptions and figures are based on preserved material, consisting of one female and one male colony bearing gonophores and four immature colonies.

Myrionema was one of a number of common forms found on Low Island which were selected by Dr. T. A. Stephenson for the determination of their breeding periods. For this purpose I undertook the weekly examination of this species during four months from March to June, and had therefore an opportunity of observing the animal closely. Some interesting details in the life-history, as seen in the living hydroid, are here recorded, as well as observations on the development as investigated by sections of specimens preserved in Bouin's fluid. Fresh material was collected every few days, and in this way most of the developmental stages were secured ; colonies did not flourish when kept under artificial conditions. Recently-hatched planulae were placed in finger-bowls in which the sea-water was changed twice a day ; it was then possible to watch their transformation into the polyp.

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* I am indebted to Dr. E. A. Briggs, of Sydney University, for the correct name of the hydroid and for referring me to the paper by Light. Dr. Briggs's report on the Hydroids will be published in Vol. IV of this series.

According to Light, a characteristic feature of the male is that two gonophores are commonly borne on each hydranth. Although two is certainly the most prevalent number, very many hydranths, in a colony that is obviously flourishing, bear only one; three is also quite usual (Plate I, figs. 1 and 2), whilst rarely even four are present. The gonophore consists of two, three or four chambers (Plate I, figs. 1 and 2), sometimes only one, and, as
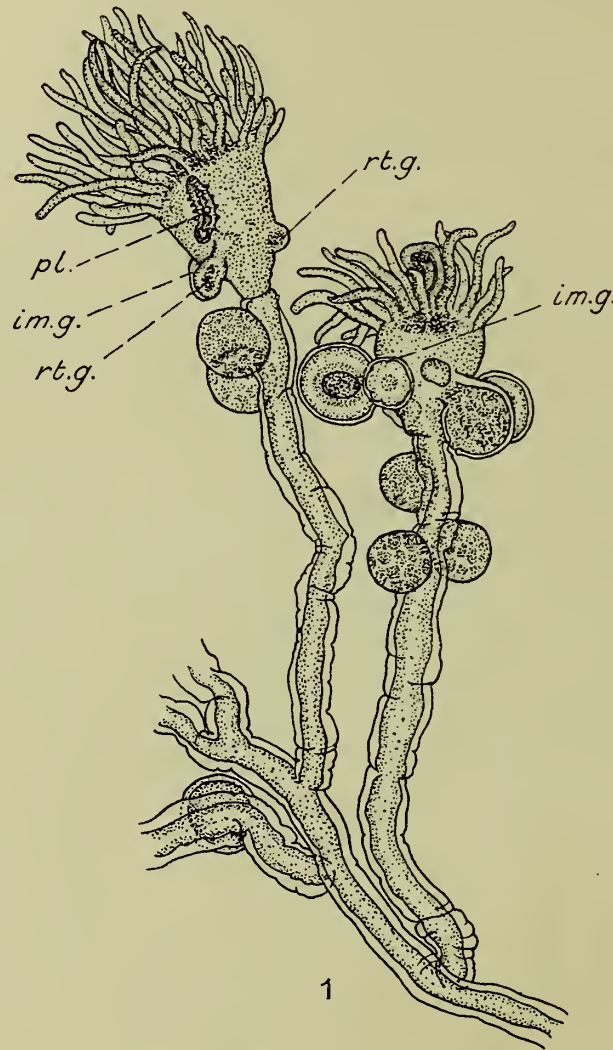

TEXT-FIG. 1.—Drawing of a cleared preparation from part of a female colony showing two hydranths. One bears a very immature gonophore (*im.g.*) and two embryos fixed to its stalk; the remains of two depleted gonophores (*rt.g.*) project from the body, and within the coelenteron is a small polychaete (*pl.*). The second hydranth has three embryos fixed alternately down the stalk and a fourth is just ready to be attached; two well-developed gonophores and one immature one (*im.g.*) are borne on its body.   × 25.

recorded by Light, it may be bifurcated at the tip. Active spermatozoa were observed in gonophores of all sizes.

In the female, four to six gonophores to a hydranth is the typical condition, but in some colonies a much greater number may be seen crowded round the lower portion of the polyp. In the specimen figured (Plate I, fig. 3) ten well-developed gonophores were

counted ; seven were very commonly present, and these may be at different stages of development, as for example in one case where five occurred round the hydranth, of which two were not fully formed, whilst an additional three were in the act of being placed upon the stalk immediately below. Variable numbers of gonophores are shown in Text-figs. 1 to 4.

The process by which the ovum reaches the stalk is an interesting one. The gonophore, when fully developed, consists of a hollow outgrowth of the hydranth containing
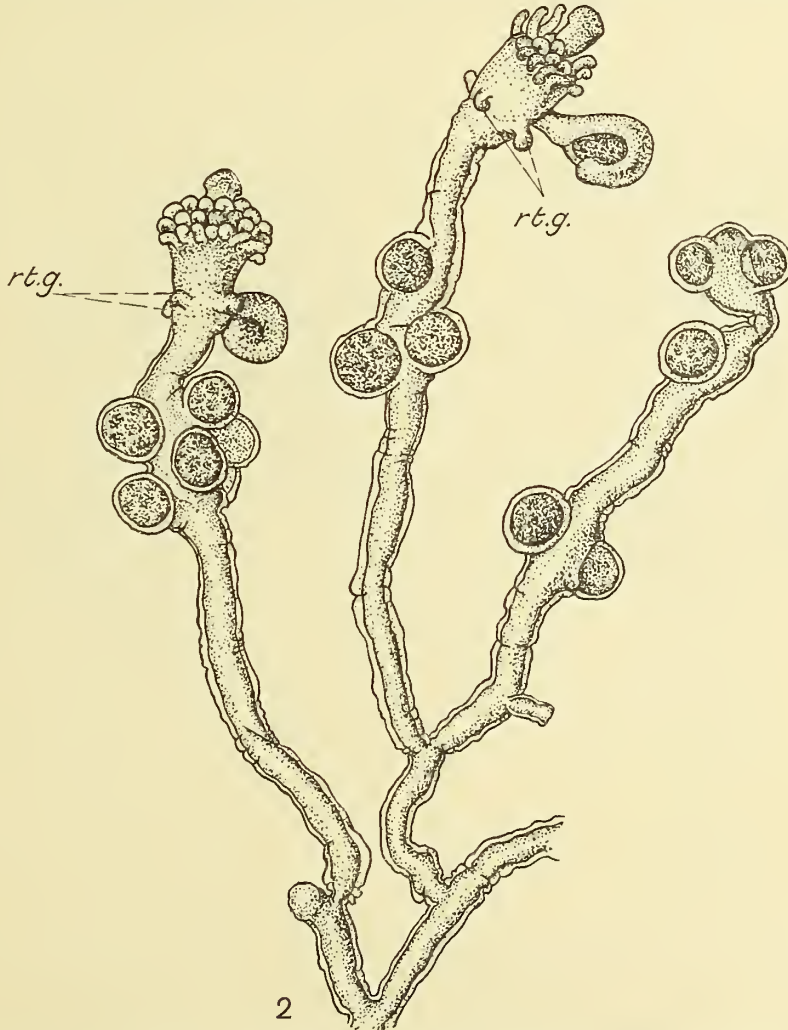

TEXT-FIG. 2.—Drawing of part of a preserved colony showing three stalks carrying a variable number of embryos ; their gonophores are reduced to mere stumps (*rt.g.*), which project from the body of the two hydranths. Each hydranth bears a well-developed gonophore. The hydranth has disappeared from the third stalk.   × 25.

both ectoderm and entoderm, between which is an extremely thin layer of mesogloea. The entodermal spadix encircles the ovum in the shape of a horseshoe, at the open end of which the ovum is only separated from the exterior by a thin layer of ectoderm, very much as figured by Allman (1871) (Plate XIII, fig. 6) for *Eudendrium ramosum*. On reaching a certain stage, the pedicel of the gonophore bends downwards so as to press the open side of the spadix against the hydrocaulus, the thin layer of ectoderm in this

region simultaneously disappearing, apparently by actual rupture, and possibly also by partial disintegration. The ovum thus exposed adheres immediately to the perisarc of the stem by the tough capsule it has by this time secreted around itself. The spadix simultaneously contracts so that its two layers come into contact and its cavity is obliterated (Plate II, fig. 7, *sp.*); the empty gonophore now springs back to its former position as a transparent cap (Text-figs. 3 and 4), which shrinks rapidly, and all that remains is a short stump which projects from the body of the hydranth for some time afterwards (Text-figs. 1 and 2, *rt.g.*). I have never seen any part of the depleted gonophore drop off;
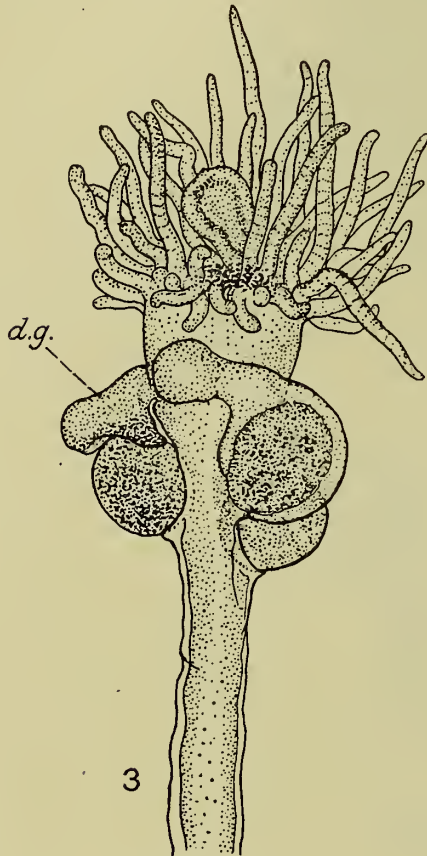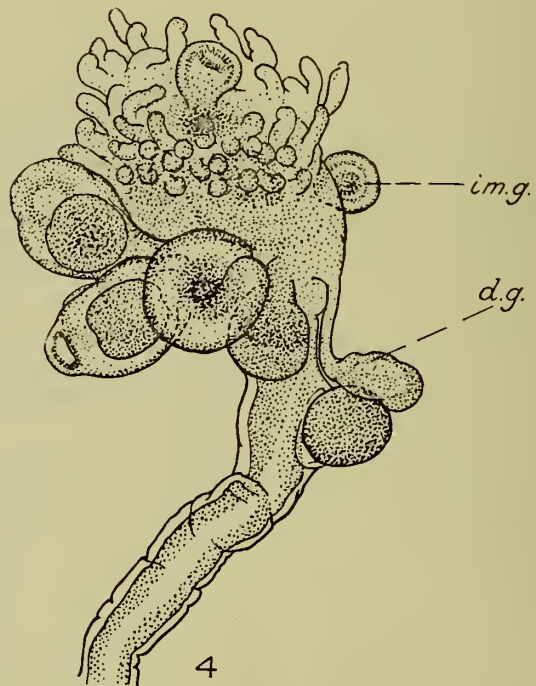
Text-fig. 3.   Text-fig. 4.

Text-fig. 3.—Drawing of a cleared preparation of a female hydranth, showing an ovum which has just become fixed to the stalk. The empty gonophore (*d.g.*) is springing back as a transparent cap. A second ovum is about to be placed on the stalk (the pecidel has been displaced to one side by the coverslip), and a third embryo is already attached to it. × 40.

Text-fig. 4.—Drawing of a cleared preparation of a female hydranth, showing a relaxed gonophore with a lengthened pedicel (*d.g.*). Seven other gonophores are present, two of which are only indicated behind the hydranth; all are well developed except one (*im.g.*), which is quite small. × 40.

the cord-like spadix becomes withdrawn into the hydranth and the ectoderm shrivels markedly, whilst both layers appear to undergo a considerable amount of degeneration. The ova may be affixed to the stalk in an irregular ring just below the hydranth (Text-fig. 2) or alternately down the stem (Text-figs. 1 and 2), the latter being the more usual method. In order to attach the ovum at lower levels the pedicel of the gonophore lengthens so that the requisite position may be reached (Text-fig. 4), the hydranth itself often

bending over at the same time, thus aiding in the operation. This process is certainly not due to early atrophy of the polyp as suggested by Light, for gonophores at varying stages of development frequently occur around the same hydranths (Text-figs. 1 and 4). Some may be quite small, others large, and yet others may have already deposited their ova down the stem. When all these have been placed on the stalk the hydranth frequently dies off, but by no means always. In one interesting example, where two embryos were developing on the stalk, the hydranth was not only flourishing, but young ova were observed in the ectoderm, a short distance below these embryos. It may be noted also that the polyp shown in Text-fig. 1 was actively feeding, as shown by the polychaete in its coelenteron.

I have not attempted in this paper to go into the question of the origin of the germ-cells, whether they arise from the ectoderm or the entoderm—a point about which in hydroid there is still much difference of opinion. The question is not of much importance, however, as Goette (1907) has shown that the place of origin differs according to the genus or even according to the species, and that in *Eudendrium* it may perhaps vary in one and the same species. In *Myrionema* both large and smaller ova each containing a reticular nucleus and a conspicuous nucleolus are to be seen along the stalks of the hydranths ; everyone of these lies in the ectoderm close against the mesogloea (Plate I, fig. 4a, ov.). In a developing bud (Plate I, fig. 4, ov.) or in the fully formed polyp (Plate I, fig. 5, ov.), on the other hand, ova are invariably found within the entoderm. Similar observations have been made by Congdon (1906) in *Eudendrium hargitti*, and therefore this author concludes that the egg must pass through the mesogloea at the neck of the hydranth. There is no doubt that the ova do penetrate through the mesogloea in this region, for I have actually seen the migration taking place. Plate I, fig. 5, shows a transverse section through the stalk just below the hydranth ; lying in the ectoderm is an ovum from which pseudopodial processes extend out into the entoderm, the mesogloea having disappeared along this area. Migration from the ectoderm into the entoderm has been described in several hydroids, but the actual penetration through the mesogloea has not always been observed, and it usually occurs when the egg is at an earlier stage, and therefore much smaller in size than in *Myrionema*.

Great difficulty was experienced in trying to follow the development of the egg into the planula. C. W. Hargitt (1904) found it impossible to make out the early cleavage stages in *Eudendrium ramosum* owing to the apparently complete disappearance of the nucleus. The same phenomenon occurs in *Myrionema*, and here observations are rendered much more difficult by the presence of algal cells. These zooxanthellae have already been described by Light (1913). They are present in large numbers at the base of the entoderm cells and are crowded together in the tentacles. Ova lying in the ectoderm of the stalk very rarely contain zooxanthellae—actually in one case only were such cells seen within the ovum at this stage, and the infection was already well established, for no less than 23 to 24 algae were counted—but as soon as the ovum passes into the entoderm of the hydranth numerous algal cells come to lie within the cytoplasm. Once within the gonophore they undergo multiplication, obscuring still further the inconspicuous nuclear divisions.

Many staining methods were tried, the zooxanthellae standing out well after safranin counterstained with gentian violet and iodine (Gram's method), and still better after Volkonsky's stain ; safranin with Wasserblau, and also iron brazelin were found useful ;

but on the whole iron haematoxylin gave the best results, preferably the quick method, care being taken that the yolk was left quite pale in colour.

On reaching the entoderm of the hydranth the outline of the egg becomes indistinct and tends to merge into the surrounding entoderm cells. Not only zooxanthellae, but entoderm cells also appear to become incorporated into the cytoplasm of the ovum. These entoderm cells are exceedingly small and it was impossible to follow their subsequent fate, but very probably they contribute towards the formation of yolk, as they are known to do in some other hydroids. It may be noted here that occasionally a few ectoderm cells appear to be present in the cytoplasm of young ova which are migrating along the stalk, but the part, if any, these play in later development it is impossible to say. As soon as the ovum becomes enclosed within the gonophore, yolk increases very rapidly in amount, but I have no definite evidence that the entoderm cells of the spadix participate in this increase, as inferred by C. W. Hargitt (1904). Entoderm cells can be distinguished round the periphery of the egg during accumulation of yolk, but soon their identification is no longer possible. The zooxanthellae are at first also scattered near the margin (Plate II, fig. 6, z.), and may be rather more numerous about the nucleus of the ovum.

The yolk soon divides up into small spheres, a mass of compact yolk forming in the centre (Plate II, fig. 6), but by the time the egg is ready to leave the gonophore this central portion has also split into spheres. The nucleus, which has a conspicuous nucleolus and a fine chromatin network, originally lies near the centre, but when a large quantity of yolk has been produced, it passes to the margin of the ovum (Plate II, fig. 6, n.). The nuclear membrane very soon breaks down, the nucleolus disappears and the nuclear contents disperse as fragments, and all traces of these are lost. This condition, however, only lasts for a very brief period ; almost as soon as, or even before, the partition of yolk into spheres is complete and the ovum has become attached to the stalk, irregular patches of proto-plasm of comparatively large size are visible between the spheres (Plate II, fig. 7). In many of these definite chromosomes are discernible, whilst stages of mitosis can be recognized (Plate II, fig. 8). From the protoplasmic masses amoeboid processes extend out, and these continue into delicate prolongations which penetrate between the spheres, constituting a slender reticulum. This network is not easy to follow, but most probably it is present throughout the egg, uniting the protoplasmic masses. The yolk spheres gradually collect together into a number of circular clumps, in each of which are included a few algal cells, and within each also one of the protoplasmic masses is usually to be seen (Plate II, fig. 9). In all likelihood every ball of yolk spheres contains such a mass, although I was unable to demonstrate its presence in every case. On bursting the capsule in living material these balls were mistaken for early blastulae, each composed of a number of cells, but sections subsequently showed that apart from zooxanthellae the supposed cells were simply spheres of yolk, the protoplasmic masses and strands not being easily perceptible, and, moreover, were not suspected at the time.

As development proceeds within the capsule the embryo becomes more solid, the yolk-balls unit together, and the protoplasm spreads out more evenly throughout the egg. Eventually it tends to accumulate round the margin, at first in an ill-defined manner (Plate III, fig. 11), but gradually becoming transformed into a distinct ectodermal layer (Plate III, fig. 12), which originates at one side or another, and by degrees develops round the entire surface. During the formation of the ectoderm an irregular cavity appears in the centre of the embryo. The capsule now very soon ruptures (Plate III, fig. 13), and the

larva creeps out as a planula (Plate III, fig. 14), the central cavity rapidly enlarging. This takes place only a few days—the exact number was not definitely determined—after the capsule is fixed to the stalk of the hydranth. The planula never swims freely in the
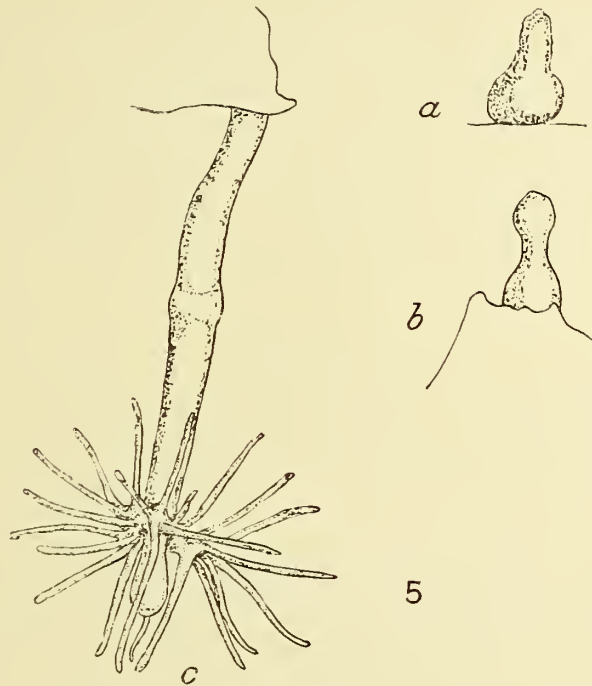
TEXT-FIG. 5.—Drawing of a living young hydroid, specimen B. *a*, The pear-shaped planula immediately after fixation, 24 hours after hatching ; *b*, the same, $30\frac{1}{2}$ hours after hatching ; *c*, the same, 5 days after hatching, when it measured about 2 mm. from the base to the tip of the hypostome.

water, but slowly creeps by means of mucus secreted by cells of the ectoderm, and drops on to neighbouring plants or on to other *Myrionema*, or apparently may crawl along the stalk of the parent colony. It is difficult to be quite sure that cilia are absent, but certainly after careful observations none were detected. Movement is at all events very
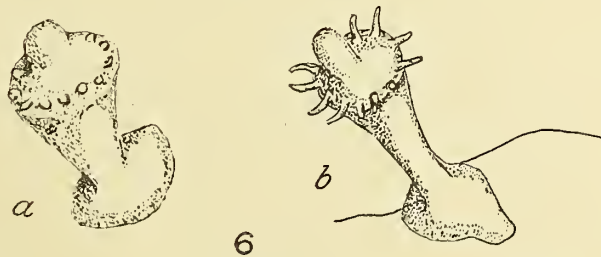
TEXT-FIG. 6.—Drawing of a living young hydroid, specimen A. *a*, 24 hours after hatching ; $30\frac{1}{2}$ hours after hatching.

restricted, and if a suitable surface on which a planula can attach itself is not almost directly reached, it soon perishes. Favoured by a convenient substratum it becomes pear-shaped and then fixes itself by the broad end (Text-fig. 5, *a*). At this end a cone-shaped plug of entoderm (Plate III, fig. 14) can be seen for some time projecting into the

central cavity.   The time taken for further growth varies slightly, at least when confined within a finger-bowl.   The fixed end spreads out, and at about 24 hours after hatching the young hydroid assumes the shape seen in Text-fig. 5, *a*, and may even have developed tentacular buds (Text-fig. 6, *a*).   Text-figs. 5 and 6 show two specimens which fastened themselves to a small piece of *Halimeda* weed, specimen A having developed rather more quickly than specimen B.   The latter is depicted in Text-fig. 5, *c*, five days after hatching, when it measured about 2 mm. from the tip of the hypostome to the base of the animal. Owing probably to unfavourable conditions the head of A died off between three and four days after hatching, but nine or ten days later a new head was found to be developing, which in 24 hours showed a distinct hypostome and a circlet of small tentacular knobs ; two days afterwards, however, degeneration again set in and no further regeneration occurred.

DISCUSSION.

The development of *Myrionema* shows a striking resemblance to that described in *Distichopora* by Hickson (1893).   There the nucleus migrates to the edge of the gonophore, the nuclear membrane disappears and the nuclear contents are scattered throughout the ovum.   Islands of protoplasm next appear in the yolk, and these are connected by a very coarse network of fine protoplasmic strands ; later these islands become more numerous and the network finer.   A syncytium is eventually formed round the periphery from which the ectoderm is differentiated.   Nests of yolk similar to those seen in *Myrionema* are described and figured, but in *Distichopora* this segmentation is believed to affect the yolk only, for the nuclei are always distributed between the aggregations of yolk.

C. W. Hargitt (1904) has given an account of the development of *Eudendrium ramosum*, and in many details it corresponds to that of *Myrionema*.   Hargitt describes the massing of the yolk towards the centre of the gonophore, due as he thinks to formation of yolk round the periphery by the metabolism of the entodermal cells of the gonophore.   In *Myrionema* also entoderm cells seemingly become enclosed within the egg and presumably participate in the genesis of yolk, but as already mentioned, it is uncertain if the actual spadix takes part in this process.   A similar migration of the nucleus to the margin and subsequent fragmentation occurs in *Eudendrium ramosum*, but there a cytoplasmic reticulum still remains throughout the egg, no such reticulum being observed in *Myrionema* at this stage.   The accumulation of yolk into balls also takes place, and only in some of them were nuclear centres discernible, so that division of the yolk here likewise appears to have some relation to the protoplasm.   The large masses of protoplasm often containing nuclear divisions, so conspicuous in *Myrionema* and corresponding so closely to those figured for *Distichopora* by Hickson, are not definitely described for *Eudendrium ramosum*. The ectoderm is formed as in *Myrionema*, but the larva is ciliated and has a longer free-swimming life, up to three days, and probably owing to this fact the entoderm is not differentiated so early—not until near the time of fixation.

The shifting of the nucleus to the periphery of the egg and the subsequent discharge of the nuclear constituents is a common phenomenon in hydroids, and is closely related to the process of maturation and of fertilization.   Neither maturation nor fertilization were observed in *Myrionema* ; quite possibly fertilization takes place at night, as discovered by Benoit (1925) in *Myriothela*.

The zooxanthellae (Plate II, fig. 10) in *Myrionema* are most numerous in the tentacles,

but are present in large numbers in the entoderm of the polyp and along the stem ; they occur more sparingly in the hypostome and in the entodermal lobes round the base of the hypostome. In all these situations they can be seen undergoing division into two, the pyrenoid first and then the nucleus. In some specimens division into three also takes place, especially in the tentacles where multiplication is most active, the nucleus of one of the daughter cells undergoing a second division. In this connection it is noteworthy that the zooxanthellae present among the yolk spheres of the developing embryo often lie in groups of three cells. Division into four was never observed anywhere.

Zooxanthellae very similar to those found in *Myrionema* have been described and figured in *Millepora* by Mangan (1909). A pyrenoid can always be seen surrounded by a clear space, and the nucleus is spherical with closely packed chromatin granules. The cell membrane did not respond to cellulose tests, and it may be noted that in *Myrionema* it was found impossible to get the wall to take on the usual cellulose stains. In *Myrionema* the algal cells pass into the ovum as soon as the latter begins to migrate into the entoderm, and there soon multiply rapidly ; in *Millepora* they lie in the vacuolated substance of the manubrium, and from thence pass directly into the ovum, here undergoing division into two, and occasionally four cells. As already stated, division into four was never seen in *Myrionema*.

As early as 1882 Hamann figured the green cells moving from the entoderm through the mesogloea into the egg of *Hydra viridis*, and later workers (Hadzi, 1906 ; Goetsch, 1919) have confirmed these observations. In 1911, Hadzi showed that the xanthellae in *Halecium ophiodes*, penetrating the mesogloea, make their way from the entoderm of the gonophore into the egg. The most recent investigator (Haffner, 1925) of *Chlorohydra viridissima* (formerly *H. viridis*) has demonstrated very clearly (Text-fig. 16, p. 43) the manner in which large numbers of chlorellae migrate from the entoderm through the mesogloea to the ovum. It has been mentioned that in an isolated case in *Myrionema* zooxanthellae were present within an ovum which lay in the ectoderm of the stalk ; these must have travelled through the mesogloea, so that a method of infection similar to that in *Hydra* may occur very exceptionally in *Myrionema* also.*

In his original description of *Myrionema* Pictet (1893) gives the colour as yellow-green. In the same species from Ceylon green cells comparable with *Chlorella vulgaris* have been described by Svedelius (from Oltmann, 1923). It is thus evident that *Myrionema amboinense* may contain either zoochlorellae or zooxanthellae according to the locality in which it is found.

I am much indebted to Miss Joyce Townend for the drawings of Text-figs. 1 to 4 and of Plate I, fig. 3. I have also to thank Mr. F. J. Pittock, of University College, for the microphotographs, Plate I, figs. 1 and 2.

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* I understand that Dr. Briggs has occasionally observed algae in the ectoderm.

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DESCRIPTION OF PLATE I.

FIG. 1.—Photograph of a male hydranth bearing three ripe gonophores, one composed of 3, the other two of 4 chambers. × 20.

FIG. 2.—Microphotograph of a cleared specimen of a male hydranth bearing three gonophores, one composed of 4, and two of 3 chambers. × 30.

FIG. 3.—Drawing of a female hydranth bearing ten fully developed gonophores, of which eight are visible, in whole or part. × 25.

FIG. 4.—Longitudinal section through a bud showing three ova (*ov.*) lying within the entoderm. A few zooxanthellae (*z.*) are seen in the cytoplasm of the ova. × 110.

FIG. 4a. Transverse section through the stalk a short distance below fig. 4, showing an ovum (*ov.*) lying in the ectoderm. × 110.

FIG. 5.—Section passing obliquely through a hydranth and transversely through the stalk immediately below it. One ovum (*ov.*) is seen lying in the entoderm, and another has just passed into a developing gonophore (*g.*). In both the nucleus is shown, and numerous zooxanthellae (*z.*) lie in the cytoplasm. An ovum (*ov.*) lies in the ectoderm of the stalk and from it pseudopodial processes are penetrating into the entoderm, the mesogloea having disappeared in this region. One zooxanthella (*z.*) has already passed into the cytoplasm. × 110.
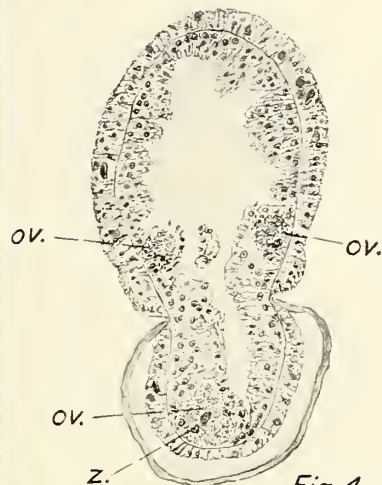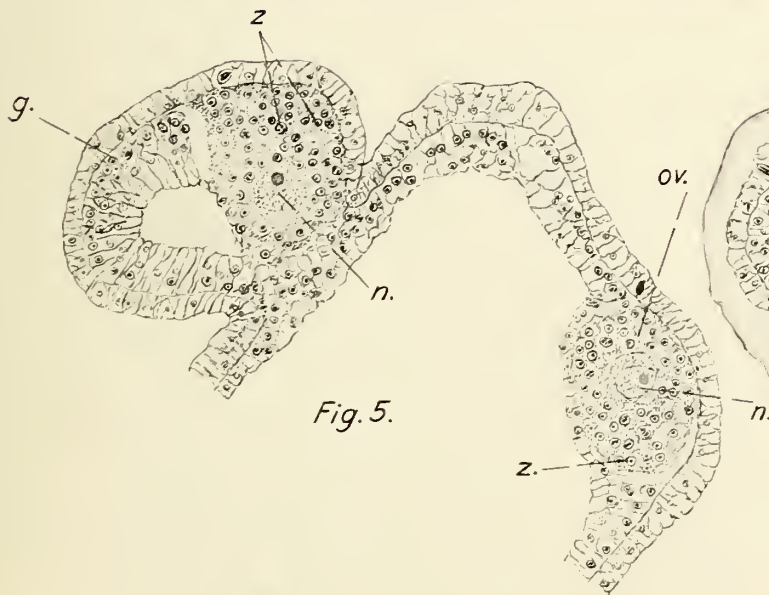
GREAT BARRIER REEF EXPEDITION 1928–29.

Brit. Mus. (Nat. Hist.).   REPORTS, VOL. III, No. 4.   PLATE I.
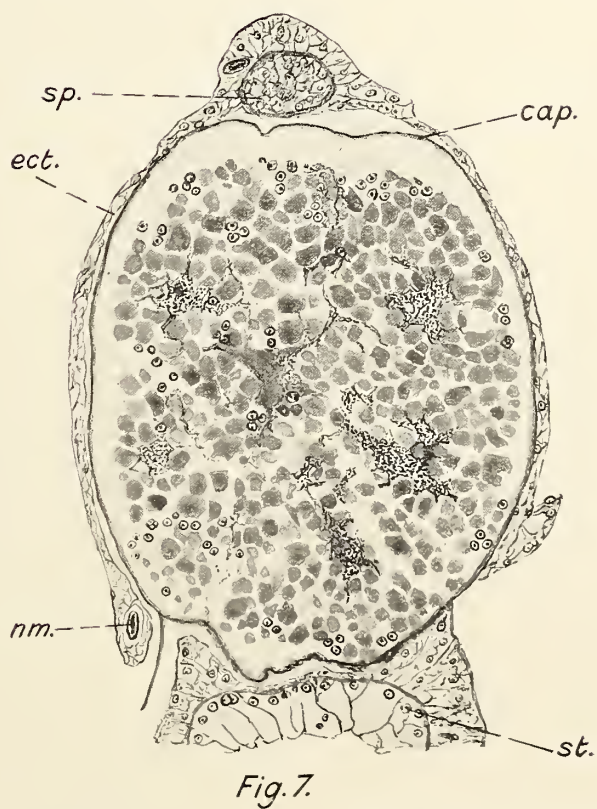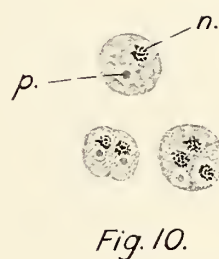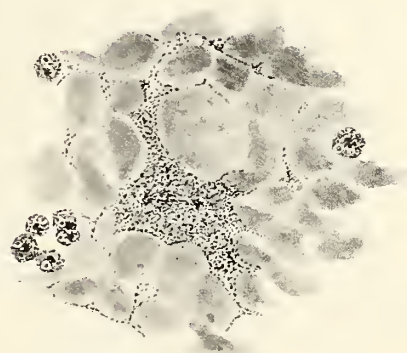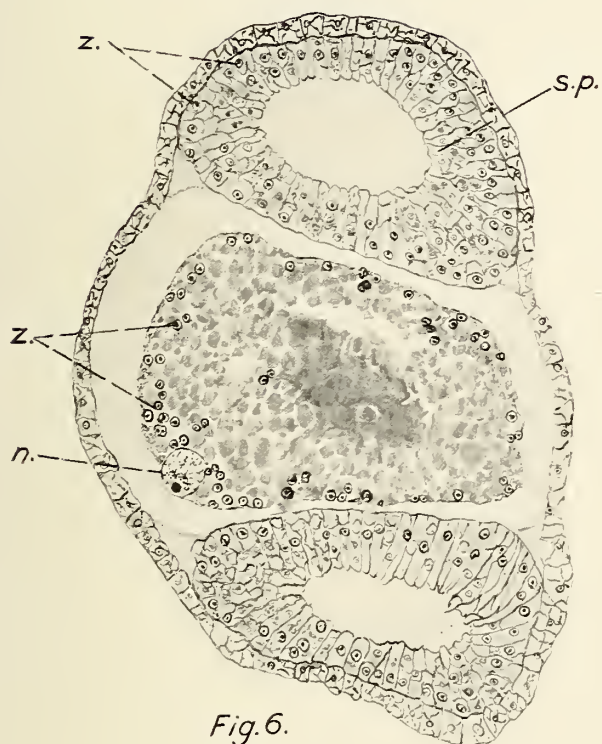
Fig. 4a.

Fig. 1.

Fig. 4.

Fig. 5.
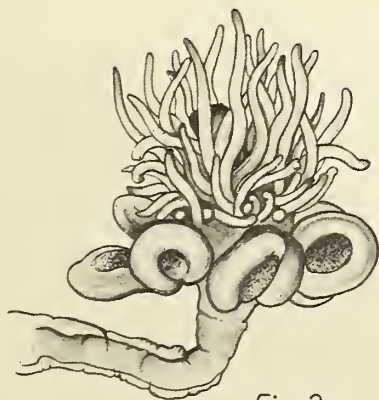
Fig. 3.

Fig. 2.

DESCRIPTION OF PLATE II.

FIG. 6.—Section through a fully developed gonophore, showing the hollow thick-walled spadix (*sp.*) surrounded by the ectoderm. Within lies the ovum. The nucleus (*n.*), showing a well-marked nucleolus, has migrated to the margin, and the yolk consists of a central mass surrounded by yolk-spheres. The zooxanthellae (*z.*) are seen round the circumference. × 200.

FIG. 7.—Section through a developing embryo immediately after its attachment to the stalk. Large protoplasmic masses can be seen among the yolk spheres, and in some of these chromosomes or masses of chromatin are present. Zooxanthellae (*z.*) are scattered among the yolk. The ectoderm (*ect.*) of the gonophore is retracting and the spadix (*sp.*) is reduced to a solid cord of cells. *cap.* = capsule. *nem.* = nematocyst. *st.* = stalk. × 200.

FIG. 8.—Section through a protoplasmic mass a few sections behind fig. 7, showing a telophase of mitosis. Several zooxanthellae (*z.*) are drawn, containing a darkly staining nucleus and a well-marked pyrenoid. Some are undergoing division. × 600.

FIG. 9.—Section through an embryo at a later stage than Fig. 7. The yolk-spheres have collected into a number of balls, within some of which protoplasm containing chromatin is visible. *st.* = stalk. × 200.

FIG. 10.—Three zooxanthellae. One is undergoing division into two, and in another there are three nuclei. *n.* = nucleus. *p.* = pyrenoid. × about 1200.

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Fig. 6.

Fig. 8.

Fig. 10.

Fig. 9.

Fig. 7.

DESCRIPTION OF PLATE III.

FIG. 11.—Section through a later stage than fig. 9. The protoplasm is now beginning to accumulate round the periphery of the embryo, especially at one side. × 200.

FIG. 12.—Section through an embryo in which a definite layer of ectoderm has formed round the side adjacent to the stalk. A central cavity has made its appearance. × 200.

FIG. 13.—Section through a planula about to hatch. The ectoderm is well developed and laden with mucus-cells, and there is a well-marked central cavity. The capsule is ruptured at one side, and opposite this area mucus is being actively secreted; this strongly suggests that mucus plays a part in the dissolution of the capsule. × 200.

FIG. 14.—Lonigtudinal section of a planula immediately after hatching. A plug of entoderm is seen projecting into the cavity at one end. × 110.

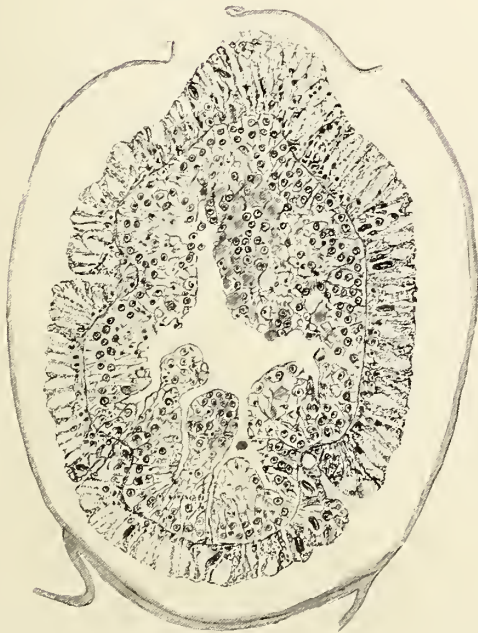GREAT BARRIER REEF EXPEDITION 1928–29.

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Fig. 11.

Fig. 12.

Fig. 13.

Fig. 14.